

<https://helda.helsinki.fi>

Apparent survival, territory turnover and site fidelity rates in Northern Goshawk *Accipiter gentilis* populations close to the northern range limit

Tolvanen, Jere

2017

Tolvanen , J , Pakanen , V-M , Valkama , J & Tornberg , R 2017 , ' Apparent survival, territory turnover and site fidelity rates in Northern Goshawk *Accipiter gentilis* populations close to the northern range limit ' , Bird Study , vol. 64 , no. 2 , pp. 168-177 . <https://doi.org/10.1080/00063657.2017.1309351>

<http://hdl.handle.net/10138/310845>

<https://doi.org/10.1080/00063657.2017.1309351>

unspecified

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

1 Apparent survival, territory turnover and site fidelity rates in Northern Goshawk
2 *Accipiter gentilis* populations close to northern range limit

3

4 Jere Tolvanen¹, Veli-Matti Pakanen¹, Jari Valkama² and Risto Tornberg¹

5

6

7 ¹ Department of Ecology and Genetics, University of Oulu, P.O. Box 3000, FI-90014 University of
8 Oulu, Finland.

9 ² Finnish Museum of Natural History, P.O. Box 17, FI-00014 University of Helsinki, Finland

10

11

12 Short title: Goshawk survival & site fidelity

13

14

15 **Keywords:** Capture-mark-recapture, sex-specific apparent survival, breeding dispersal, raptor

16

17

18 Corresponding author:

19 Jere Tolvanen

20 Email: jere.tolvanen@oulu.fi

21

22 **Summary**

23 **Capsule:** Mark-recapture data suggest low apparent survival and sex- and population-specific site
24 fidelity and territory turnover in adult Northern Goshawks *Accipiter gentilis* breeding in northern
25 Europe.

26 **Aims:** Understanding how species cope with global environmental change requires knowledge of
27 variation in population demographic rates, especially from populations close to the species'
28 northern range limit and from keystone species such as raptors. We analyze apparent survival and
29 breeding dispersal propensity of adult Northern Goshawks breeding in northern Europe.

30 **Methods:** We used long-term mark-recapture data from two populations in Finland, northern
31 Europe, and Cormack-Jolly-Seber models and binomial GLMs to investigate sex- and population-
32 specific variation in apparent survival, territory turnover and site fidelity.

33 **Results:** We report low apparent survival (53–72%) of breeding adult goshawks. Breeding dispersal
34 propensity was higher in females than males, especially in northern Finland, contrasting previous
35 studies that suggest high site fidelity in both sexes.

36 **Conclusion:** Low apparent survival in females may be mainly due to permanent emigration outside
37 the study areas, whereas in males the survival rate may truly be low. Both demographic aspects may
38 be driven by the combination of sex-specific roles related to breeding and difficult environmental
39 conditions prevailing in northern latitudes during the non-breeding season.

40 **Introduction**

41 Populations at the edge of their distribution often face poorer conditions, and consequently suffer
42 from lower rates of reproduction and survival (e.g. Sexton *et al.* 2009, Karvonen *et al.* 2012). The
43 ongoing climate change alters environments with particularly pronounced effects being expected at
44 high latitudes and on populations living close to their northern range limit (Jetz *et al.* 2007, Virkkala
45 *et al.* 2008). Therefore, studies investigating basic demographic rates in spatially distinct
46 populations close to the species' range limit are highly valuable in understanding the future impacts
47 climate change may have (Gibson *et al.* 2009, Rehm *et al.* 2015). Unfortunately, the vast majority
48 of species lack information on different demographic rates that are crucial for understanding
49 population dynamics and population viability (Morris & Doak 2002). The most urgent need is for
50 information on survival because data for them is rare and survival rates commonly have high
51 elasticity measures implying that even small changes in survival rates may have substantial effects
52 on population demography (Gaillard *et al.* 2000, Heppell *et al.* 2000, Saether & Bakke 2000).

53

54 Understanding population dynamics of key species, such as top predators, is particularly important
55 because they often influence abundance, distribution and behaviour of several other species across
56 trophic levels (Sergio *et al.* 2008, Lima 2009). For example, raptors have a profound role in animal
57 communities through direct predation on prey populations (Norrdahl & Korpimäki 2000, Valkama
58 *et al.* 2005, Park *et al.* 2008) and indirect effects on the behaviour of prey and other predators
59 (Thomson *et al.* 2006, Sergio & Hiraldo 2008, Lima 2009, Morosinotto *et al.* 2010, Michel *et al.*
60 2016), potentially triggering trophic cascades including several trophic levels (Chakarov & Krüger
61 2010). So far, research on raptor demography has concentrated on reproduction (e.g. Byholm &
62 Kekkonen 2008, Björklund *et al.* 2015), and many raptor species lack even basic estimates of adult
63 survival (Newton *et al.* 2016), which is unfortunate as the importance of adult survival for

64 population growth increases in long-lived species such as raptors (Heppell *et al.* 2000, Saether &
65 Bakke 2000, Krüger 2007).

66

67 The Northern Goshawk (*Accipiter gentilis*, hereafter goshawk) is an example of a widely
68 distributed, relatively abundant top predator that has diverse effects on animal communities in
69 boreal forests (Tornberg 2001, Hakkarainen *et al.* 2004, Mönkkönen *et al.* 2007, Byholm *et al.*
70 2012, Tornberg *et al.* 2016). However, few studies have concentrated on goshawk demography in
71 Europe or at northern latitudes close to the species' range limit. The survival estimates reported so
72 far are based on ring recoveries (Haukioja & Haukioja 1970) or radio-telemetry methods (Kenward
73 *et al.* 1999, Tornberg and Colpaert 2001). Survival and site fidelity estimates derived from mark-
74 recapture data are almost absent for European goshawks (but see Krüger 2005). Environmental
75 conditions for goshawks are more difficult in northern latitudes both due to harsher climate (e.g.
76 colder temperature) and lower and more variable food availability (e.g. most prey species migrate
77 south for the winter). Both environmental aspects may affect survival, as has been observed in other
78 northern birds of prey (Brommer *et al.* 2002, Hakkarainen *et al.* 2002, Francis & Saurola 2004).
79 Consequently, survival in northern latitudes may differ from more southern areas, and thus survival
80 estimates from northern populations are valuable in understanding goshawk demography
81 throughout the species range.

82

83 We collected mark-recapture data by capturing goshawk adults during the breeding season in two
84 distinct geographical areas in northern Europe, where goshawks breed close (*ca.* 400–900 km) to
85 their northern range limit. We estimate apparent adult survival by using open population live
86 recapture models (Cormack-Jolly-Seber models; Lebreton *et al.* 1992). Because apparent survival is
87 confounded with permanent emigration, we evaluate its impact using time since marking models
88 and by estimating site fidelity and territory turnover rates.

89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113

Materials and methods

Study species

Goshawk is a holarctic, territorial, medium-sized raptor showing strong reversed sexual size dimorphism (Kenward 2006). The female incubates and defends the nest during the incubation (from late April to late May in our study areas) and the first half of the nestling period (from late May to late June), while the male is responsible for provisioning food. The female usually takes part in provisioning in the late nestling period (from late June to mid July). Diet consists of small- and medium-sized birds and mammals (Tornberg 1997, Drennan 2006). Typical nesting habitat is mature forest with large trees, high canopy closure and open understories (Penteriani 2002). The residency status of goshawks varies between populations from resident (Boal *et al.* 2003) to either seasonally (Squires & Ruggiero 1995) or partially migratory (Kenward *et al.* 1981, Underwood *et al.* 2006). In Finland, adult goshawks are usually resident, but may occasionally disperse hundreds of kilometres (R. Tornberg unpubl. radio telemetry data, Saurola *et al.* 2013). The conservation status of goshawks is ‘Near Threatened’ in Finland (abundance estimate 8600 individuals; Tiainen *et al.* 2016) and ‘Least Concern’ in Europe (332 000–440 000 mature individuals; BirdLife International 2016).

Study areas

Our study was conducted in two study areas in Finland. The northern study area (hereafter northern Finland, NF) is located around the city of Oulu (65°N, 25°E; ca. 2200 km²) and consists of coastal lowlands, including the island of Hailuoto in the Baltic sea. The area belongs to the middle boreal vegetation zone. A mosaic of forests and mostly drained bogs covers about two thirds of the area. Forests consist of managed conifer or mixed stands dominated by scots pine (*Pinus sylvestris*) and

114 Norwegian spruce (*Picea abies*) mixed with deciduous species (*Betula sp.*, *Populus tremula*).
115 Agricultural areas and human settlements are concentrated on the coast of the Baltic sea and river
116 valleys.

117

118 The southern study area (hereafter southern Finland, SF) consists of two subareas located southeast
119 from the city of Pori (61°N, 22°E; ca. 2550 km²) and around the city of Turku (61°N, 22°E; ca. 600
120 km²). The area is also coastal lowland, located in the southern boreal and hemiboreal vegetation
121 zones ca. 500 km southwest of the NF study area. Landscape is a mixture of forests and agricultural
122 areas. Forests consist of spruce dominated coniferous stands mixed with pine, birches and aspen.

123

124 *Mark-recapture data*

125 Breeding goshawk populations have been monitored since 1994 and 1993 in northern and southern
126 Finland, respectively. A territory was defined as a cluster of alternative nest sites and surrounding
127 area used and defended by a goshawk pair (Steenhof & Newton 2007). All known territories were
128 visited between April and May to determine occupancy. A territory was considered occupied if
129 fresh signs of occupation (prey remains, moulted feathers, faeces etc.) were observed near the nest
130 sites (Steenhof & Newton 2007). If no signs were found, suitable nearby forest sites were searched
131 for new nest site. Because majority of the forests in our study areas are too young (due to forest
132 management) for goshawk nesting, we used aerial photographs to identify potential new nesting
133 sites and focused our searching efforts on them. This maximized the use of limited resources
134 available for nest searching. The total area of nest search varied depending on the amount of
135 suitable habitat, but usually searching occurred within a kilometre from the old nest site. Nest
136 search was performed by walking slowly within a forest patch in transects ca. 50 m apart to cover
137 the whole patch while carefully looking for new nest structures or other signs of goshawk activity.
138 We also used playbacks of goshawk vocalizations to locate new breeding pairs and nest sites

139 (Andersen 2007). Pairs were defined as breeding if at least one egg was laid. Nestlings were ringed
140 at age of 15–30 days.

141

142 Since 1999 in NF and 2002 in SF, breeding adults have been caught at the breeding sites using a
143 raptor net with a mounted eagle owl (*Bubo bubo*) as a lure. Birds were sexed on the basis of size
144 (Kenward 2006) and marked with individually numbered aluminium leg bands. During the early
145 and late years capture efforts or success were relatively low that could compromise survival
146 estimation. Therefore, we restrict the survival analyses to study periods when capture efforts were
147 highest, i.e. to 2003-2012 in NF and 2005-2011 in SF study area. Survival analysis data sets
148 included 91 individuals and 127 captures in NF and 120 individuals and 163 captures in SF. Site
149 fidelity and territory turnover analyses were based on the full study periods (1999-2016 in NF,
150 2002-2016 in SF).

151

152 *Survival analysis*

153 We used Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965, Lebreton *et*
154 *al.* 1992) to estimate apparent survival of breeding adult goshawks. CJS models simultaneously
155 estimate both apparent survival and recapture probability (the probability that a living individual is
156 recaptured/encountered in the study area) and therefore account for temporary emigration of
157 individuals (Lebreton *et al.* 1992). The resulting survival estimates may nevertheless be confounded
158 with permanent emigration outside the study area, therefore the estimate is termed "apparent
159 survival". Survival analyses included sex (male vs. female) and time since marking (TSM; newly
160 marked individuals vs. individuals marked in previous years; Pradel *et al.* 1997) as categorical
161 explanatory variables. Since the SF study area consisted of two subareas, the subarea variable
162 (Turku vs. Pori) was included in the analysis of the SF data set.

163

164 We kept model structures simple due to small sample sizes. A maximum of three explanatory
165 variables were simultaneously incorporated into a model (two for survival, one for recapture; except
166 for the global models). Interactions and temporal variation were not considered. All explanatory
167 variables were fitted both alone and additively to each of the other variables in the survival model
168 structure. Model structure with constant survival was also applied. Recapture probability model
169 structure included either sex or subarea, or the recapture probability was kept constant. All survival
170 structures were fitted with all different recapture structures, resulting in the total number of 8 and 22
171 candidate models for the NF and SF data sets, respectively (global models included).

172

173 For the NF data, the global model included additive effects of sex and TSM in survival (S) and the
174 effect of sex in recapture (p) model structures [S(Sex+TSM) p(Sex)]. For the SF data set the global
175 model included also the additive effect of subarea in both survival and recapture model structures
176 [S(Subarea+Sex+TSM) p(Subarea+Sex)]. Goodness of fit testing of the global models and
177 estimation of variance inflation factors (\hat{c}) were done using the parametric bootstrap approach
178 provided in program MARK (White & Burnham 1999, White *et al.* 2001). The global models fit
179 both data sets (NF: $p = 0.202$; SF: $p = 0.486$). Slight over-dispersion was corrected for in NF data (\hat{c}
180 $= 1.17$), but in SF data it was not necessary ($\hat{c} = 1.00$). Ranking of the candidate models was based
181 on Akaike's Information Criterion corrected for small sample size, and over-dispersion in NF data,
182 (AICc or QAICc; Akaike 1974, Burnham & Anderson 2002). We quantified the importance of
183 different explanatory variables in explaining the variation in apparent survival and recapture
184 probabilities using the sum of model-specific Akaike weights over all the models that included the
185 specific variable (Burnham & Anderson 2002). In addition, since some explanatory variables were
186 incorporated in a varying number of models, we also calculated the average Akaike weight for each
187 variable. Apparent survival and recapture probability estimates and associated unconditional 95%
188 confidence intervals were derived via model averaging over all relevant models (see results for

189 details). All survival analyses were performed in program MARK 8.0 (White & Burnham 1999,
190 White *et al.* 2001).

191

192 *Site fidelity and territory turnover*

193 We calculated site fidelity and turnover rates with two approaches. The first approach included
194 individuals caught in successive years. Site fidelity is the percentage of individuals that stayed on
195 the same territory in successive years, and turnover is the percentage of observations where a
196 breeding individual was replaced by another individual on a territory in successive years. These are
197 the traditional approaches used to estimate site fidelity and territory turnover (see e.g. Bechard *et al.*
198 2006, Reynolds & Joy 2006).

199

200 However, estimates based on the traditional approaches may be biased for several reasons. First, if
201 an individual, captured at year t , breeds in the same known territory the next year ($t+1$), it is more
202 likely to be recaptured than an individual, which disperses to a new territory, possibly outside the
203 study area or to an unknown territory within the study area. Furthermore, if it is possible to capture
204 individuals only if they are successful in breeding (as is the case in this study) and if breeding
205 success and dispersal propensity are interrelated (e.g. Haas 1998, Hoover 2003, Jiménez-Franco *et*
206 *al.* 2013), it may be impossible to capture a dispersing individual in successive years even when the
207 new territory is known. All above-mentioned possibilities support the expectation of obtaining
208 disproportionally more data on site-faithful than on dispersing individuals, i.e. the traditional site
209 fidelity estimates may be biased high. Turnover is based on individuals captured in the same
210 territory, and thus is not biased by dispersal to unknown territories. However, based on our present
211 goshawk data, if a breeding male disappears from its territory, it is rarely replaced immediately by
212 another male. For example in the NF data, in 19 of the 28 cases where the territorial male was
213 replaced, the territory remained unoccupied for at least one year before the new male occupied the

territory. Therefore, male turnover seldom occurs in successive years, which results in low turnover estimates if the traditional estimation approach is used.

To alleviate the above-mentioned issues we also estimated site fidelity and turnover by including successive captures of individuals (site fidelity), or successive captures within territories (turnover), regardless of the number of years between the captures. These estimates may in turn be biased low (site fidelity) or high (turnover) due to the inclusion of observations with up to nine years between successive captures. The true site fidelity and turnover estimates probably lie somewhere between the two estimates. The estimates of site fidelity and turnover include only one observation per individual/territory.

Generalized linear models (logit link function, binomial error distribution) were used to investigate differences in site fidelity and turnover estimates between males and females in both study areas and between the two study areas within both sexes. Site fidelity and turnover estimates based on both approaches were analysed separately. Statistical significance of the sex or area differences was evaluated by likelihood ratio tests. In the case of the estimates based on the second approach (variable number of years between the captures), the number of years between the captures was included as an additional covariate (centred to the mean; termed 'Years'). The fit of the models to the observed data (overdispersion in binomial models) was assessed by the ratio of residual deviance to the degrees of freedom of the model. If this ratio does not substantially exceed unity, the model with binomial error structure fits well to the data (Collett 2003). Program R 3.3.1 (R Development Core Team 2016) was used for the analyses.

Results

239 *Apparent adult survival*

240 In northern Finland, apparent survival of breeding adult goshawks was best explained by time since
241 marking (TSM; Tables 1 and 2). However, when comparing the mean Akaike weights of the
242 explanatory variables, a constant survival rate was equally supported as the TSM effect (Table 1). It
243 is unknown whether the individuals, when they were captured for the first time, were also breeding
244 for the first time. However, of the territories where an individual was captured for the first time,
245 79% had contained breeding pairs for one year at the most before their capture indicating that most
246 of the individuals captured for the first time were also breeding for their first or second time.
247 Therefore the two TSM groups are hereafter called ‘early-career breeders’ and ‘experienced
248 breeders’. Model averaged apparent survival probability estimates were 0.534 (95% CI [0.292,
249 0.760]) for early-career breeders and 0.675 (95% CI [0.503, 0.810]) for experienced breeders
250 (Figure 1; estimates based on models 1a, 2a, 5a and 7a, Table 2). Survival probability did not differ
251 between males and females. The model averaged survival estimates were 0.533 (95% CI [0.293,
252 0.758]) in early-career and 0.669 (95% CI [0.485, 0.812]) in experienced males, while they were
253 0.555 (95% CI [0.262, 0.814]) in early-career and 0.689 (95% CI [0.467, 0.849]) in experienced
254 females (estimates based on all models, Table 2). Recapture probability was consistently explained
255 by sex across all survival model structures (Tables 1 and 2). Model averaged recapture probability
256 was higher for males (0.496, 95% CI [0.270, 0.724]) than females (0.207, 95% CI [0.065, 0.493];
257 estimates based on all models, Table 2).

258

259 In southern Finland, the variable subarea received the most support in explaining apparent survival
260 of goshawks (Table 1) being included in the top six models (Table 3). Model averaged apparent
261 survival probability was 0.715 (95% CI [0.442, 0.888]) in the Turku subarea and 0.534 (95% CI
262 [0.382, 0.680]) in the Pori subarea (estimates based on models 1b, 6b, 8b, 11b, 14b and 19b, Table
263 3). Differences in survival between males and females were small; model averaged estimates were

0.741 (95% CI [0.454, 0.908]) for males and 0.661 (95% CI [0.349, 0.876]) for females in Turku, and 0.555 (95% CI [0.389, 0.709]) for males and 0.458 (95% CI [0.235, 0.700]) for females in Pori (estimates based on models 1b, 2b, 4b–6b, 8b, 10b, 11b, 12b, 14b, 17b and 19b, Table 3). TSM effect was not supported (Table 1). Sex was the most important variable explaining recapture probability (Table 1). Model averaged recapture probability was 0.359 (95% CI [0.208, 0.544]) for males and 0.249 (95% CI [0.098, 0.504]) for females (estimates based on models 1b–4b, 6b–10b, 14b, 16b–18b and 22b, Table 3).

271

Site fidelity and territory turnover

Both estimation approaches indicated high site fidelity in male goshawks in both northern (approach 1: 1.000, n = 17; approach 2: 0.909, n = 22) and southern Finland (approach 1: 1.000, n = 19; approach 2: 0.966, n = 29; Figure 2a). Site fidelity was lower in females than in males in northern Finland (approach 1: 0.500, n = 6; approach 2: 0.615, n = 13; Table 4, Figure 2a), but not in southern Finland (approach 1: 0.900, n = 10; approach 2: 0.938, n = 16). Female site fidelity was also lower in northern Finland compared to southern Finland (Figure 2a), though not quite significantly so for the estimation approach 1 (Table 4).

280

Turnover rates of males were similar in northern (approach 1: 0.077, n = 13; approach 2: 0.560, n = 25) and southern Finland (approach 1: 0.053, n = 19; approach 2: 0.314, n = 35; Table 4, Figure 2b). In northern Finland, turnover rate was higher in females (approach 1: 0.667, n = 9; approach 2: 0.789, n = 19) than in males (Table 4, Figure 2b). Female turnover was also higher in northern Finland than in southern Finland (approach 1: 0.250, n = 12; approach 2: 0.400, n = 25; Table 4; Figure 2b), although the difference based on the approach 1 remained barely nonsignificant (Table 4). Overdispersion levels were acceptable in all models (residual deviance/df \leq 1.313).

288

289

290 **Discussion**

291 We report the first apparent adult survival estimates based on mark-recapture data in goshawks
292 breeding close to their northern range limit. We found relatively low adult survival with no apparent
293 differences between northern and southern Finland or between sexes. Mean survival estimates for
294 different sexes and areas varied between 0.46 and 0.74, a range which is at the low end reported in
295 previous mark-recapture or radio telemetry studies (0.62–0.86; Table 5). The survival estimates in
296 the Pori subarea in southern Finland (males 0.56, females 0.46) were especially low. The reason for
297 the very low (potentially unrealistically low) survival estimates in Pori is currently unknown.
298 Considering the size of goshawks (*ca.* 1 kg) they could be predicted to have a mean survival of 0.80
299 (Newton *et al.* 2016), higher than found in this study.

300

301 Recapture probabilities of goshawks were generally low, at maximum 0.50, a problem also
302 prevalent in previous studies (DeStefano *et al.* 1994, Kennedy 1997, Reynolds *et al.* 2004). Low
303 recapture probabilities reflect the general difficulty of capturing goshawks. Especially females are
304 usually less aggressive than males in attacking the eagle owl lure used in capture attempts. Higher
305 breeding dispersal probability could also result to temporary emigration, and thus further explain
306 the low recapture probabilities of females.

307

308 The relatively low adult survival estimates reflect either true survival or alternatively a higher
309 degree of permanent emigration (Sandercock 2006). We used estimates of site fidelity and territory
310 turnover to evaluate the possibility of permanent emigration. We found high site fidelity in males in
311 both study areas (91–100%) and in females in southern Finland (90–94%) but lower in females in
312 northern Finland (50–62%). Turnover rates mirrored site fidelity being particularly high in females
313 in northern Finland (67–79%) compared to females in southern Finland (25–40%) or males in

314 overall (5–56%). Turnover of females in northern Finland was also remarkably high in comparison
315 to North American goshawk populations (males 23%-25%; females 16%-30%; Detrich &
316 Woodbridge 1994, Bechard *et al.* 2006, Reynolds & Joy 2006). Site fidelity and turnover estimates
317 are lacking for European goshawk populations, but Krüger (2005) noted that in female goshawks in
318 Germany breeding dispersal was observed only twice (74 females followed) during the 30-year
319 study period implying high site fidelity.

320

321 Overall, it appears that at least the apparent survival estimates of females in northern Finland were
322 confounded with permanent emigration outside the study areas. In northern Finland, survival tended
323 to be lower for early-career breeders (53%) than for experienced breeders (68%). Given the site
324 fidelity and turnover estimates, permanent emigration could be the prevailing explanation for the
325 very low early-career apparent survival for females, but the same explanation appears unlikely for
326 males. If permanent emigration is the sole explanation for the low early-career survival rates, TSM
327 effect could be expected to be stronger for females than for males. However, we did not initially fit
328 any interaction models and thus could not observe the potential interactive effects between sex and
329 TSM. *Post hoc* fitting of sex*TSM interaction model indicated that the TSM effect might be more
330 pronounced in females (apparent survival estimates: 0.47 in early-career and 0.67 in experienced
331 males, and 0.41 in early-career and 0.80 in experienced females; based on model
332 $S(\text{sex}*\text{TSM})p(\text{sex})$). The sex*TSM interaction effect was nevertheless far from significant ($\beta=-$
333 0.926, 95% CI [-4.012, 2.161]), probably due to the small sample size.

334

335 An alternative explanation for the low apparent early-career survival, and perhaps the more
336 probable one regarding males, is that breeding is such a demanding task for the new recruits that
337 many of them die during the next non-breeding season. In goshawks, the male is almost solely
338 responsible for providing food for both the female and nestlings (Kenward 2006). As a result, males

339 might be in too bad condition at the start of the potentially harsh winter conditions (cold weather,
340 low prey availability, short day-length) to survive through to the next spring. Only the highest
341 quality individuals may survive to breed in the next year, and in further years as suggested by the
342 relatively higher apparent survival of experienced breeders. In addition, males probably benefit
343 from holding the same territory year-round, because site familiarity should enhance their
344 provisioning capabilities during breeding (Kenward 2006). That may hinder their possibilities for
345 movements outside the territory even during the non-breeding season. Females may, in contrast,
346 counter the difficult winter conditions by increasing their movement beyond the territory boundaries
347 (e.g. in search of prey), and consequently they may also end up breeding in another territory. This
348 could at least partly explain the lower site fidelity and higher turnover of females than males,
349 especially in northern Finland where the winter conditions are even more challenging than in
350 southern Finland (Pirinen *et al.* 2012). Nevertheless, we cannot exclude the possibility that also
351 some male dispersal events resulted to permanent emigration, and thus to low apparent survival.
352 Likewise, low female early-career survival could also partly reflect truly low survival.

353

354 Yet another explanation for the difference between the early-career (or individuals captured for the
355 first time) and experienced breeders could be that individuals dispersed from the study area due to
356 the capture and handling *per se*. However, for this to be the case, the same pattern could have been
357 expected to appear also in southern Finland (capture method was identical in both areas), but TSM
358 did not explain apparent survival there. Hence, the differences in apparent survival in northern
359 Finland most likely reflect natural patterns.

360

361 In conclusion, apparent survival rates of goshawks in Finland were relatively low, and probably at
362 least partly confounded with permanent emigration. Apparently the most reliable survival estimates
363 were obtained for males, but even they were relatively low in comparison to previous studies. In

364 northern Finland, females apparently exhibited frequent breeding dispersal, a previously
365 undiscovered behaviour in goshawks, despite having been frequently observed in birds in general
366 (e.g. Greenwood 1980, Pakanen *et al.* 2015). Both the low survival rates of males and high dispersal
367 propensity of females may be related to sex-specific roles in breeding and territorial behaviour as
368 well as to challenging environmental conditions during winter. In other raptors and owls adverse
369 weather conditions do affect survival (Francis & Saurola 2004, Reichert *et al.* 2010, Franke *et al.*
370 2011), and in the goshawk harsh winters result in decreased breeding density in the next season
371 (Tornberg *et al.* 2013), potentially due to weather-related variation in survival. Further
372 investigations of weather effects on goshawk survival and dispersal propensity are warranted with
373 data spanning for longer time periods than in our study (Grosbois *et al.* 2008).

374

375 **Acknowledgements**

376 We are thankful to Teemu Honkanen, and Jukka and Jouko Kivelä for collecting a considerable part
377 of the data of southern Finland. Comments from two anonymous reviewers improved the
378 manuscript. Funding was provided by the Natural History Society of Oulu (to JT) and the
379 Zoological Museum of the University of Oulu (to JT and RT).

380

381 **References**

- 382 **Akaike, H.** 1974. New look at the statistical model identification. *IEEE Transactions on Automatic*
 383 *Control AC* **19**: 716–723.
- 384 **Andersen, D.E.** 2007. Survey techniques. In Bird, D.M. & Bildstein, K.L. (ed.) *Raptor research*
 385 *and management techniques*, Raptor Research Foundation, Hancock House Publishers, USA.
- 386 **Bechard, M.J., Fairhurst, G.D. & Kaltenecker, G.S.** 2006. Occupancy, productivity, turnover,
 387 and dispersal of northern goshawks in portions of the northeastern Great Basin. *Stud. Avian*
 388 *Biol.* **31**: 100–108.
- 389 **BirdLife International.** 2016. *Accipiter gentilis*. The IUCN Red List of Threatened Species 2016:
 390 e.T22695683A93522852. [http://dx.doi.org/10.2305/IUCN.UK.2016-](http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22695683A93522852.en)
 391 [3.RLTS.T22695683A93522852.en](http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22695683A93522852.en). Downloaded on 19 December 2016.
- 392 **Björklund, H., Valkama, J., Tomppo, E. & Laaksonen, T.** 2015. Habitat effects on the breeding
 393 performance of three forest-dwelling hawks. *PLoS ONE* **10**: e0137877.
- 394 **Boal, C.W., Andersen, D.E. & Kennedy, P.L.** 2003. Home range and residency status of northern
 395 goshawks breeding in Minnesota. *Condor* **105**: 811–816.
- 396 **Boal, C.W., Andersen, D.E. & Kennedy, P.L.** 2005. Productivity and mortality of northern
 397 goshawks in Minnesota. *J. Raptor Res.* **39**: 222–228.
- 398 **Brommer, J.E., Pietiäinen, H. & Kolunen, H.** 2002. Reproduction and survival in a variable
 399 environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. *Auk* **119**: 544–550.
- 400 **Burnham, K.P. & Anderson, D.R.** 2002. *Model selection and multimodel inference: a practical*
 401 *information-theoretic approach*. 2nd edn. Springer, New York, USA.
- 402 **Byholm, P., Burgas, D., Virtanen, T. & Valkama, J.** 2012. Competitive exclusion within the
 403 predator community influences the distribution of a threatened prey species. *Ecology* **93**:
 404 1802–1808.

- 405 **Byholm, P. & Kekkonen, M.** 2008. Food regulates reproduction differently in different habitats:
 406 experimental evidence in the goshawk. *Ecology* **89**: 1696–1702.
- 407 **Chakarov, N. & Krüger, O.** 2010. Mesopredator release by an emergent superpredator: a natural
 408 experiment of predation in a three level guild. *PLoS ONE* **5**: e15229.
- 409 **Collett, D.** 2003. *Modelling binary data*. 2nd edn. Chapman & Hall/ CRC, Florida, USA.
- 410 **Cormack, R.M.** 1964. Estimates of survival from the sighting of marked animals. *Biometrika* **51**:
 411 429–438.
- 412 **DeStefano, S., Woodbridge, B. & Detrich, P.J.** 1994. Survival of northern goshawks in the
 413 southern Cascades of California. *Stud. Avian Biol.* **16**: 133–136.
- 414 **Detrich, P.J. & Woodbridge, B.** 1994. Territory fidelity, mate fidelity, and movements of color-
 415 marked northern goshawks in the southern Cascades of California. *Stud. Avian Biol.* **16**: 130–
 416 132.
- 417 **Drennan, J.E.** 2006. Northern goshawk food habits and goshawk prey species habitats. *Stud. Avian*
 418 *Biol.* **31**: 198–218.
- 419 **Francis, C.M. & Saurola, P.** 2004. Estimating components of variance in demographic parameters
 420 of Tawny Owls, *Strix aluco*. *Animal Biodiversity and Conservation*. **27.1**: 489–502.
- 421 **Franke, A., Therrien, J.-F., Descamps, S. & Bêty, J.** 2011. Climatic conditions during outward
 422 migration affect apparent survival of an arctic top predator, the peregrine falcon *Falco*
 423 *peregrinus*. *J. Avian Biol.* **42**: 544–551.
- 424 **Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toïgo, C.** 2000. Temporal
 425 variation in fitness components and population dynamics of large herbivores. *Annu. Rev.*
 426 *Ecol. Syst.* **31**: 367–393.
- 427 **Greenwood, P.J.** 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim.*
 428 *Behav.* **28**: 1140–1162.

429 **Gibson, S.Y., Van Der Marel, R.C. & Starzomski, B.M. 2009.** Climate change and conservation
 430 of leading-edge peripheral populations. *Conserv. Biol.* **23**: 1369–1373.

431 **Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P.
 432 & Weimerskirch, H. 2008.** Assessing the impact of climate variation on survival in
 433 vertebrate populations. *Biol. Rev.* **83**: 357–399.

434 **Haas, C.A. 1998.** Effects of prior nesting success on site fidelity and breeding dispersal: An
 435 experimental approach. *Auk* **115**: 929–936.

436 **Hakkarainen, H., Korpimäki, E., Koivunen, V. & Ydenberg, R. 2002.** Survival of male
 437 Tengmalm's owls under temporally varying food conditions. *Oecologia* **131**: 83–88.

438 **Hakkarainen, H., Mykrä, S., Kurki, S., Tornberg, R. & Jungell, S. 2004.** Competitive
 439 interactions among raptors in boreal forests. *Oecologia* **141**: 420–424.

440 **Haukioja, E. & Haukioja, M. 1970.** Mortality rates of Finnish and Swedish goshawks (*Accipiter*
 441 *gentilis*). *Finnish Game Research* **31**: 13–20.

442 **Heppell, S.S., Caswell, H. & Crowder, L.B. 2000.** Life histories and elasticity patterns:
 443 perturbation analysis for species with minimal demographic data. *Ecology* **81**: 654–665.

444 **Hoover, J.P. 2003.** Decision rules for site fidelity in a migratory bird, the prothonotary warbler.
 445 *Ecology* **84**: 416–430.

446 **Jiménez-Franco, M.V., Martinez, J.E., Pagán I. & Calvo, J.F. 2013** Factors determining
 447 territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraetus pennatus*. *J.*
 448 *Ornithol.* **154**: 311–318.

449 **Jetz, W., Wilcove, D.S. & Dobson, A.P. 2007.** Projected impacts of climate and land-use change
 450 on the global diversity of birds. *PLoS Biol.* **5**: 1211–1219.

451 **Jolly, G.M. 1965.** Explicit estimates from capture-recapture data with both death and immigration-
 452 stochastic model. *Biometrika* **52**: 225–247.

453 **Karvonen, J., Orell, M., Rytönen, S., Broggi, J. & Belda, E.** 2012. Population dynamics of an
 454 expanding passerine at the distribution margin. *J. Avian Biol.* **43**: 102–108.

455 **Kennedy, P.L.** 1997. The northern goshawk (*Accipiter gentilis atricapillus*): Is there evidence of a
 456 population decline? *J. Raptor Res.* **31**: 95–106.

457 **Kenward, R.E.** 2006. *The goshawk*. T & A D Poyser, London, UK.

458 **Kenward, R.E., Marcström, V. & Karlbom, M.** 1981. Goshawk winter ecology in Swedish
 459 pheasant habitats. *J. Wildl. Manage.* **45**: 397–408.

460 **Kenward, R.E., Marcström, V. & Karlbom, M.** 1999. Demographic estimates from radio-
 461 tagging: Models of age-specific survival and breeding in the goshawk. *J. Anim. Ecol.* **68**:
 462 1020–1033.

463 **Krüger, O.** 2005. Age at first breeding and fitness in goshawk *Accipiter gentilis*. *J. Anim. Ecol.* **74**:
 464 266–273.

465 **Krüger, O.** 2007. Long-term demographic analysis in goshawk *Accipiter gentilis*: the role of
 466 density dependence and stochasticity. *Oecologia* **152**: 459–471.

467 **Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R.** 1992. Modeling survival and
 468 testing biological hypotheses using marked animals: A unified approach with case studies.
 469 *Ecol. Monogr.* **62**: 67–118.

470 **Lima, S.T.** 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the
 471 risk of predation. *Biol. Rev.* **84**: 485–513.

472 **Michel, V.T., Jiménez-Franco, M.V., Naef-Daenzer, B. & Gruebler, M.U.** 2016. Intraguild
 473 predator drives forest edge avoidance of a mesopredator. *Ecosphere* **7**: e01229.

474 **Morris, W.F. & Doak, D.F.** 2002. *Quantitative conservation biology: theory and practice of*
 475 *population viability analysis*. Sinauer Associates Inc, Sunderland, USA.

- 476 **Morosinotto, C., Thomson, R.L. & Korpimäki, E.** 2010. Habitat selection as an antipredator
477 behaviour in a multi-predator landscape: all enemies are not equal. *J. Anim. Ecol.* **79**: 327–
478 333.
- 479 **Mönkkönen, M., Husby, M., Tornberg, R., Helle, P. & Thomson, R.L.** 2007. Predation as a
480 landscape effect: the trading off by prey species between predation risks and protection
481 benefits. *J. Anim. Ecol.* **76**: 619–629.
- 482 **Newton, I., McGrady, M.J. & Oli, M.K.** 2016. A review of survival estimates for raptors and
483 owls. *Ibis* **158**: 227–248.
- 484 **Norrdahl, K. & Korpimäki, E.** 2000. Do predators limit the abundance of alternative prey?
485 Experiments with vole-eating avian and mammalian predators. *Oikos* **91**: 528–540.
- 486 **Pakanen, V.-M., Lampila, S., Arppe, H. & Valkama, J.** 2015. Estimating sex specific apparent
487 survival and dispersal of Little Ringed Plovers (*Charadrius dubius*). *Ornis Fennica* **92**: 172–
488 186.
- 489 **Park, K.J., Graham, K.E., Calladine, J. & Wernham, C.W.** 2008. Impacts of birds of prey on
490 gamebirds in the UK: a review. *Ibis* **150** (Suppl. 1): 9–26.
- 491 **Penteriani, V.** 2002. Goshawk nesting habitat in Europe and North America: A review. *Ornis*
492 *Fennica* **79**: 149–163.
- 493 **Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J-P., Karlsson, P. & Ruuhela, R.** 2012.
494 *Climatological statistics of Finland 1981-2010*. Reports 2012: 1. Finnish Meteorological
495 Institute. Helsinki, Finland. 96 pp.
- 496 **Pradel, R., Hines, J.E., Lebreton, J.-D. & Nichols, J.D.** 1997. Capture-recapture survival models
497 taking account of transients. *Biometrics* **53**: 60–72.

498 **R Development Core Team.** 2016. R: A language and environment for statistical computing. - R
 499 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL
 500 <http://www.R-project.org/>.

501 **Rehm, E.M., Olivas, P., Stroud, J. & Feeley, K.J.** 2015. Losing your edge: climate change and
 502 the conservation value of range-edge populations. *Ecol. Evol.* **5**: 4315–4326.

503 **Reichert, B.E., Martin, J., Kendall, W.L., Cattau, C.E. & Kitchens, W.M.** 2010. Interactive
 504 effects of senescence and natural disturbance on the annual survival probabilities of snail
 505 kites. *Oikos* **119**: 972–979.

506 **Reynolds, R.T. & Joy, S.M.** 2006. Demography of northern goshawks in northern Arizona, 1991-
 507 1996. *Stud. Avian Biol.* **31**: 63–74.

508 **Reynolds, R.T., White, G.C., Joy, S.M. & Mannan, R.W.** 2004. Effects of radiotransmitters on
 509 northern goshawks: Do tailmounts lower survival of breeding males? *J. Wildl. Manage.* **68**:
 510 25–32.

511 **Saether, B.-E. & Bakke, Ø.** 2000. Avian life history variation and contribution of demographic
 512 traits to the population growth rate. *Ecology* **81**: 642–653.

513 **Sandercock, B.K.** 2006. Estimation of demographic parameters from live encounter data: a
 514 summary review. *J. Wildl. Manage.* **70**: 1504–1520.

515 **Saurola, P., Valkama, J. & Velmala, W.** 2013. The Finnish Bird Ringing Atlas. Vol. 1. - Finnish
 516 Museum of Natural History and the Ministry of Environment, Helsinki.

517 **Seber, G.A.** 1965. A note on the multiple-recapture census. *Biometrika* **52**: 249–259.

518 **Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K. & Hiraldo,**
 519 **F.** 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy.
 520 *Annu. Rev. Ecol. Evol. Syst.* **39**: 1–19.

521 **Sergio, F. & Hiraldo, F.** 2008. Intraguild predation in raptor assemblages: a review. *Ibis* **150**
 522 **(Suppl. 1):** 132–145.

- 523 **Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. 2009.** Evolution and ecology of species
524 range limits. *Annu. Rev. Ecol. Evol. Syst.* **40**: 415–436.
- 525 **Squires, J.R. & Ruggiero, L.F. 1995.** Winter movements of adult northern goshawks that nested in
526 southcentral Wyoming. *J. Raptor Res.* **29**: 5–9.
- 527 **Steenhof, K. & Newton, I. 2007.** Assessing nesting success and productivity. In Bird, D.M. &
528 Bildstein, K.L. (ed.) *Raptor research and management techniques*, Raptor Research
529 Foundation, Hancock House Publishers, USA.
- 530 **Thomson, R.L., Forsman, J.T., Sardà-Palomera, F. & Mönkkönen, M. 2006.** Fear factor: prey
531 habitat selection and its consequences in a predation risk landscape. *Ecography* **29**: 507–514.
- 532 **Tiainen, J., Mikkola-Roos, M., Below, A., Jukarainen, A., Lehikoinen, A., Lehtiniemi, T.,**
533 **Pessa, J., Rajasärkkä, A., Rintala, J., Sirkiä, P. & Valkama, J. 2016.** Suomen lintujen
534 uhanalaisuus 2015 – The 2015 Red List of Finnish Bird Species. Ympäristöministeriö &
535 Suomen ympäristökeskus.
- 536 **Tornberg, R. 1997.** Prey selection of the goshawk *Accipiter gentilis* during the breeding season:
537 The role of prey profitability and vulnerability. *Ornis Fennica* **74**: 15–28.
- 538 **Tornberg, R. 2001.** Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in
539 northern Finland. *Wildlife Biol.* **7**: 245–256.
- 540 **Tornberg, R. & Colpaert, A. 2001.** Survival, ranging, habitat choice and diet of the northern
541 goshawk *Accipiter gentilis* during winter in northern Finland. *Ibis* **143**: 41–50.
- 542 **Tornberg, R., Lindén, A., Byholm, P., Ranta, E., Valkama, J., Helle, P. & Lindén, H. 2013.**
543 Coupling in goshawk and grouse population dynamics in Finland. *Oecologia* **171**: 863–872.
- 544 **Tornberg, R., Rytkönen, S., Välimäki, P., Valkama, J. & Helle, P. 2016.** Northern goshawk
545 (*Accipiter gentilis*) may improve black grouse breeding success. *J. Ornithol.* **157**: 363–370.

546 **Underwood, J., White, C.M. & Rodriguez, R.L.** 2006. Winter movement and habitat use of
547 northern goshawks breeding in Utah. *Stud. Avian Biol.* **31**: 228–238.

548 **Valkama, J., Korpimäki, E., Arroyo, B., Beja, P., Bretagnolle, V., Bro, E., Kenward, R.,**
549 **Mañosa, S., Redpath, S.M., Thirgood, S. & Viñuela, J.** 2005. Birds of prey as limiting
550 factors of gamebird populations in Europe: a review. *Biol. Rev.* **80**: 171–203.

551 **Virkkala, R., Heikkinen, R.K., Leikola, N. & Luoto, M.** 2008. Projected large-scale range
552 reductions of northern-boreal land bird species due to climate change. *Biol. Conserv.* **141**:
553 1343–1353.

554 **White, G.C. & Burnham, K.P.** 1999. Program MARK: Survival estimation from populations of
555 marked animals. *Bird Study* **46**: S120–S139.

556 **White, G.C., Burnham, K.P. & Anderson, D.R.** 2001. Advanced features of Program Mark. - In:
557 Field, R., Warren, R. J., Okarma, H. & Sievert, P. R. (ed.) *Wildlife, Land, and People:*
558 *Priorities for the 21st Century*. Proceedings of the Second International Wildlife Management
559 Congress. The Wildlife Society, Bethesda, Maryland, USA, pp 368–377.

560

561 **Tables**

562 Table 1. Relative importance of variables in explaining apparent survival and recapture probability of
 563 Northern Goshawks in northern and southern Finland. The most important variables are in bold.

Area	Parameter	Variable ^a	Sum of Akaike weights	Mean Akaike weight	Number of models
Northern	Survival	TSM	0.531	0.133	4
Finland	probability	Sex	0.307	0.077	4
		Constant	0.314	0.157	2
	Recapture	Sex	0.866	0.217	4
	probability	Constant	0.134	0.033	4
Southern	Survival	Subarea	0.744	0.083	9
Finland	probability	TSM	0.314	0.035	9
		Sex	0.405	0.045	9
		Constant	0.074	0.025	3
	Recapture	Subarea	0.157	0.022	7
	probability	Sex	0.519	0.074	7
		Constant	0.324	0.046	7

564 ^a TSM = time since marking effect (early-career breeders vs. experienced breeders); Sex = the sex effect (males vs.
 565 females); Subarea = the subarea effect within the SF study area (Turku vs. Pori); Constant = survival/recapture
 566 probability constant between individuals.

567

568 Table 2. Models of apparent adult survival of the Northern Goshawk in northern Finland.

Model ^a	Akaike		Model		
	QAICc	ΔQAICc	weight	likelihood	Parameters
1a. S(TSM)p(Sex)	177.648	0.00	0.323	1.000	4
2a. S(Constant)p(Sex)	177.903	0.26	0.285	0.880	3
3a. S(Sex)p(Sex)	179.363	1.72	0.137	0.424	4
4a. S(Sex+TSM)p(Sex)	179.608	1.96	0.121	0.375	5
5a. S(TSM)p(Constant)	181.172	3.52	0.056	0.172	3
6a. S(Sex+TSM)p(Constant)	182.319	4.67	0.031	0.097	4
7a. S(Constant)p(Constant)	182.444	4.80	0.029	0.091	2
8a. S(Sex)p(Constant)	183.467	5.82	0.018	0.055	3

569 ^a S() denotes the survival and p() the recapture model structure with the explanatory variables in parentheses. Sex = the
570 sex effect (males vs. females); TSM = time since marking effect (early-career breeders vs. experienced breeders);
571 Constant = survival/recapture probability constant between individuals.

572

573 Table 3. Models of apparent adult survival of the Northern Goshawk in southern Finland.

Model ^a			Akaike	Model	Parameters
	AICc	ΔAICc	weight	likelihood	
1b. S(Subarea)p(Sex)	246.365	0.00	0.171	1.000	4
2b. S(Subarea+Sex)p(Constant)	246.600	0.24	0.152	0.889	4
3b. S(Subarea+TSM)p(Sex)	246.635	0.27	0.149	0.874	5
4b. S(Subarea+Sex)p(Sex)	248.039	1.67	0.074	0.433	5
5b. S(Subarea+Sex)p(Subarea)	248.493	2.13	0.059	0.345	5
6b. S(Subarea)p(Constant)	248.529	2.16	0.058	0.339	3
7b. S(TSM)p(Sex)	249.128	2.76	0.043	0.251	4
8b. S(Constant)p(Sex)	249.163	2.80	0.042	0.247	3
9b. S(Subarea+TSM)p(Constant)	249.581	3.22	0.034	0.200	4
10b. S(Sex)p(Constant)	249.934	3.57	0.029	0.168	3
11b. S(Subarea)p(Subarea)	250.497	4.13	0.022	0.127	4
12b. S(Sex)p(Subarea)	250.553	4.19	0.021	0.123	4
13b. S(Subarea+Sex+TSM) p(Subarea+Sex)	250.768	4.40	0.019	0.111	7
14b. S(Constant)p(Constant)	250.895	4.53	0.018	0.104	2
15b. S(Sex+TSM)p(Subarea)	251.085	4.72	0.016	0.094	5
16b. S(Sex+TSM)p(Constant)	251.088	4.72	0.016	0.094	4
17b. S(Sex)p(Sex)	251.105	4.74	0.016	0.094	4
18b. S(Sex+TSM)p(Sex)	251.267	4.90	0.015	0.086	5
19b. S(Constant)p(Subarea)	251.576	5.21	0.013	0.074	3
20b. S(TSM)p(Subarea)	251.630	5.26	0.012	0.072	4
21b. S(Subarea+TSM)p(Subarea)	251.719	5.35	0.012	0.069	5
22b. S(TSM)p(Constant)	251.791	5.43	0.011	0.066	3

574 ^a S() denotes the survival and p() the recapture model structure with the explanatory variables in parentheses. Subarea =
575 the subarea effect within the SF study area (Turku vs. Pori); Sex = the sex effect (males vs. females); TSM = time since
576 marking effect (early-career breeders vs. experienced breeders); Constant = no variation in survival/recapture
577 probability.

578

579

580 Table 4. Model statistics of site fidelity and territory turnover rate analyses. Calculation of the response
581 variables were based on either captures in successive years (approach 1) or all successive captures regardless
582 of the number of years between the captures (approach 2), but controlling for the variable number of years
583 between the captures (parameter 'Years').

Response variable	Group	Parameter	$\chi^2_{df=1}$	p-value
Site fidelity	Males	Area	0.000	1.000
Approach 1	Females	Area	3.175	0.075
	Northern Finland	Sex	9.494	0.002
	Southern Finland	Sex	2.198	0.138
Site fidelity	Males	Area	0.514	0.473
Approach 2		Years	1.093	0.296
	Females	Area	5.994	0.014
		Years	2.013	0.156
	Northern Finland	Sex	4.877	0.027
		Years	0.576	0.448
	Southern Finland	Sex	0.209	0.648
		Years	0.038	0.845
Turnover	Males	Area	0.076	0.782
Approach 1	Females	Area	3.729	0.053
	Northern Finland	Sex	9.013	0.003
	Southern Finland	Sex	2.510	0.113
Turnover	Males	Area	1.421	0.233
Approach 2		Years	50.462	<0.001
	Females	Area	7.253	0.007
		Years	3.261	0.071
	Northern Finland	Sex	5.819	0.016
		Years	18.272	<0.001
	Southern Finland	Sex	0.100	0.752

Years

18.291

<0.001

584

585

586 Table 5. Survival probabilities estimated for different populations of the Northern Goshawk.

Location	Survival ^a	Method ^d	Years	n	Reference
Europe					
Gotland, Sweden	0.79–0.83	RT	1980–1984	78	Kenward <i>et al.</i> 1999
Germany	0.62–0.79 ^b	CMR ^c	1980–2003	74	Krüger 2005
Oulu, Finland	0.80 ^c	RT	1991–1994	19	Tornberg and Colpaert 2001
Oulu, Finland	0.53–0.68	CMR	2003–2012	91	This study
Turku, Finland	0.72	CMR	2005–2011	40	This study
Pori, Finland	0.53	CMR	2005–2011	80	This study
North America					
New Mexico, USA	0.86	CMR	1983–1995	45	Kennedy 1997
Arizona, USA	0.75	CMR	1991–2000	265	Reynolds <i>et al.</i> 2004
Minnesota, USA	0.74	RT	1998–2000	32	Boal <i>et al.</i> 2005

587 ^a Survival probabilities did not differ between males and females in any of the studies (Kennedy 1997, Kenward *et al.*
588 1999, Reynolds *et al.* 2004, this study), or they were not tested (Tornberg and Colpaert 2001, Boal *et al.* 2005).
589 Therefore, overall survival estimates are reported.

590 ^b Estimate based on females only.

591 ^c Estimate derived only for the five winter months (November–March)

592 ^d RT = radio telemetry, CMR = capture-mark-recapture(resight)

593 ^e Birds were not physically captured, but the identification of individuals was based on shed feathers.

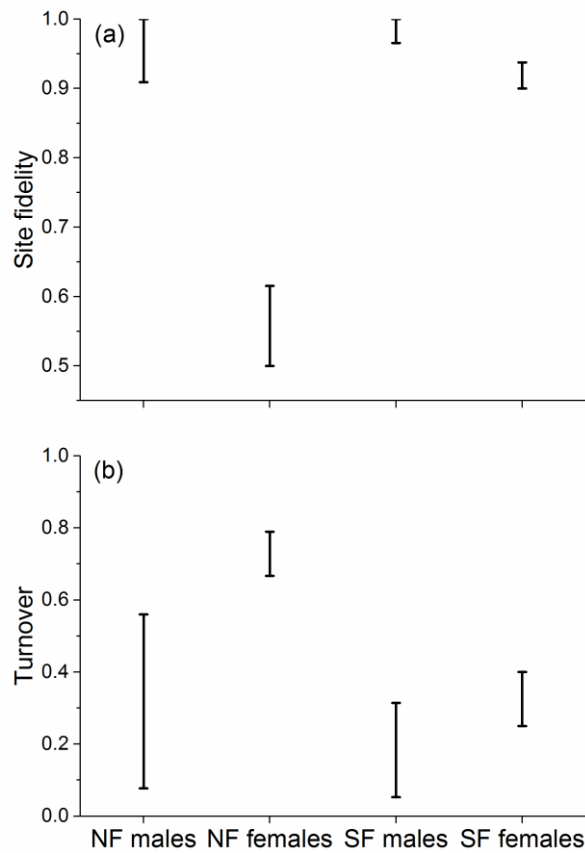
594 **Figures**

595

596

597 Figure 1. Apparent survival probability of early-career breeders and experienced breeders in northern
598 Finland (model averaged estimates \pm unconditional SEs).

599



600

601 Figure 2. Ranges of (a) site fidelity and (b) territory turnover rate estimates of male and female Northern
602 Goshawks in northern (NF) and southern (SF) Finland.